

Sympatric speciation and extinction driven by environment dependent sexual selection

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A theoretical model is studied to investigate the possibility of sympatric speciation driven by sexual selection and ecological diversification. In particular, we focus on the rock-dwelling haplochromine cichlid species in Lake Victoria. The high speciation rate in these cichlids has been explained by their apparent ability to specialize rapidly to a large diversity of feeding niches. Seehausen and colleagues, however, demonstrated the importance of sexual selection in maintaining reproductive barriers between species. Our individual-orientated model integrates both niche differentiation and a Fisherian runaway process, which is limited by visibility constraints. The model shows rapid sympatric speciation or extinction of species, depending on the strength of sexual selection.

Keywords: sympatric speciation; sexual selection; extinction; female choice; cichlids; eutrophication

1. INTRODUCTION

Female choice is believed to be the driving force behind the evolution of conspicuous male traits in many sexually reproducing animal species (Andersson 1994). In species with a non-resource-based mating system, the evolution of female preferences for costly male traits can be explained by indirect selection (Kirkpatrick & Ryan 1991; Maynard Smith 1991), either by the good-genes mechanism or by a runaway selection process (Fisher 1930; Lande 1981; Kirkpatrick 1982; Maynard Smith 1991) in which male trait and female preference are exaggerated beyond adaptivity. The direction of this runaway process is arbitrary, depending on the initial female preference distribution in the population and direct selection forces. Therefore the runaway process can cause rapid divergence of mating preferences—and thus reproductive isolation—between allopatric populations. An interesting question is whether the same process is possible within a single population, i.e. sympatrically. If so, a runaway mechanism could drive rapid sympatric speciation. Alternatively, any process impeding sexual selection could cause fusion or extinction of the newly formed species.

An interesting case to be studied here concerns the cichlid species flocks in the African great lakes, which have speciated very rapidly (Johnson *et al.* 1996; Galis & Metz 1998). As a group, the haplochromine cichlids use almost any available niche in these lakes, and their ability to adapt rapidly to different niches has been used to explain the high speciation rate in this clade (Liem 1973).

In many haplochromine cichlid species, males have bright coloration, whereas the females are cryptically coloured. This, together with the non-resource-based mating system of these cichlids, makes it likely that sexual

selection by female choice on male coloration plays a role in the evolutionary history of these fish. Indeed, Seehausen *et al.* (1997) recently demonstrated the importance of sexual selection in the speciation process by relating the disappearance of many rock-dwelling cichlid species in Lake Victoria to the increasing turbidity of the lake. As a result of eutrophication, water transparency has decreased dramatically, constraining mate choice on the basis of coloration, which was shown to be the only reproductive barrier between closely related cichlid species (Seehausen *et al.* 1998).

Here we present a theoretical model allowing for both niche differentiation and runaway processes driven by sexual selection. The model shows rapid sympatric speciation and extinction of species, depending on the visual constraints on sexual selection.

2. THE MODEL

The basic model framework is related to a previous model that demonstrated the instability of a sexual continuum (Noest 1997), although here we use an individual-orientated model instead of a partial differential equation. The model incorporates only the most basic properties of sexual selection by female choice. Furthermore, it includes an ecological niche space, in which individuals compete for resources locally. In relation to other models of sympatric speciation by sexual selection (e.g. Wu 1985; Turner & Burrows 1995), our model is characterized by the integration of sexual selection and niche differentiation and by the use of continuous instead of discrete characters.

(a) Birth and death processes

Consider a group of N individuals. Each individual I_i is characterized by a discrete character g_i denoting the gender of the individual and by three continuous characters: t_i (trait), p_i (preference) and x_i (ecological

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niche). In the cichlid case, the trait represents the light-reflection properties of the pigment in the skin of the male cichlid, whereas the preference should be interpreted as the colour preferred by the female cichlid. These three characters are assumed to be additive and fully heritable (non-heritable components will be dealt with later). We assume that the genetic variance of the three characters is stable on the time-scale covered by our model (Roughgarden 1979).

Per time-step, each individual can die with a fixed probability π_d . Moreover, individuals die as a result of competition for resources. Assuming that every individual has a resource utilization curve given by a Gaussian function with mean x_i and width σ_c , an individual I_i dies with probability

$$\pi_{\text{death},i} = \pi_d + c \sum_{j=0}^N \exp\left(-\frac{1}{2} \left(\frac{x_i - x_j}{\sigma_c}\right)^2\right), \quad (1)$$

where c represents the intensity of competition for a shared resource.

Individuals are born by sexual reproduction only. The probability of mating between female I_i and male I_j is assumed to be proportional to the attractiveness a_{ij} of the male to the female, which is taken to be a Gaussian function of niche difference (individuals occupying different niches are assumed to encounter one another less often) and discrepancy between female preference and perceived male colour.

$$a_{ij} = \exp\left(-\frac{1}{2} \left(\frac{p_i - C(t_j)}{\sigma_m}\right)^2\right) \exp\left(-\frac{1}{2} \left(\frac{x_i - x_j}{\sigma_n}\right)^2\right). \quad (2)$$

Here, σ_m is the specificity of female mate choice with respect to male colour, σ_n is the specificity of female mate choice with respect to ecological niche and C is a function mapping the male trait to a colour perceived by the female. In the cichlid case, $C(t)$ depends on the turbidity of the water. Non-heritable variance in male coloration and niche can be thought of as contributions to σ_m and σ_n .

After normalization, we write

$$\pi_{m,ij} = \frac{a_{i,j}}{\eta + \sum_{k=0, g_k=\text{male}}^N a_{i,k}} \quad (3)$$

for the probability of mating between I_i and I_j . Parameter η incorporates the Allee effect, which models the cost of finding a suitable mate. Thus, the availability of attractive males limits female offspring number, which naturally introduces a cost on female preferences.

After mating with male I_j , the female I_i produces one offspring, I_o , which, assuming that there is no genetic dominance, is characterized by

$$t_o = \frac{t_i + t_j}{2} + \xi_t, \quad (4)$$

$$p_o = \frac{p_i + p_j}{2} + \xi_p, \quad (5)$$

$$x_o = \frac{x_i + x_j}{2} + \xi_x. \quad (6)$$

The ξ_i denote samples from a normal distribution with mean 0 and width σ_i ; they represent offspring variation due to Mendelian segregation and mutation. The gender of the offspring is determined randomly with equal probabilities for male and female.

Finally, we assume weak stabilizing natural selection on male trait, representing for instance trait-dependent predation on males. The selection kernel is assumed to be a Gaussian function. For male offspring the chance of survival until reproductive age is taken to be $\exp[-t_o^2/(2\sigma_s^2)]$. This leads to a stable female-biased sex ratio. Natural selection is assumed to occur before reproductive age.

Species were distinguished by performing an agglomerative clustering procedure on the list of individuals, using the single-linkage clustering criterion and $1 - \pi_{m,ij}$ as a dissimilarity measure between individuals I_i and I_j . All clusters being more dissimilar than a threshold dissimilarity δ were considered separate species. The use of single-linkage clustering ensures that the mating probability between individuals of separate species never exceeds $1 - \delta$. Throughout this paper we take $\delta = 0.995$.

(b) Implementation

In the computer simulations, individuals were updated every time-step in a random sequence, and mortality occurred before reproduction. Females could mate with only one male every time-step. All simulations were started with ten males and ten females, all having trait, preference and niche values set to zero. Using the analytical results of Noest (1997), parameters were chosen such that ecological diversification without sexual selection could not drive speciation.

3. RESULTS

(a) The direction of evolution and the function C

The shape of the graph of the trait-to-preference mapping C , introduced in the previous section, determines the rate at which speciation and extinction occur. Here we will derive some results relating several well-defined features of trait-to-preference functions in general to the occurrence of speciation and extinction of populations evolving along these functions.

In trait-preference space, any population will evolve rapidly towards the graph of the trait-to-preference mapping C , because there male traits approximately match female preferences in the population. Let us assume that the preferences in the population are distributed with standard deviation σ around some point $(t, C(t))$ and that the inverse function C_{inv} is well defined and smooth around $C(t)$. Next, let us define \bar{t} to be the average trait value in the population and \bar{t}_p to be the trait value that is on average preferred by the females. Note that \bar{t}_p can be calculated as the average value of $C_{\text{inv}}(p)$ weighted according to the population distribution of female preference values. The difference $\Delta = \bar{t}_p - \bar{t}$ is a measure of the strength of sexual selection. To first approximation we find (G. S. van Doorn, unpublished data)

$$\Delta \approx \frac{\sigma^2 C_{\text{inv}}''(C(t))}{2!} = -\frac{\sigma^2 C''(t)}{2C'(t)^3}. \quad (7)$$

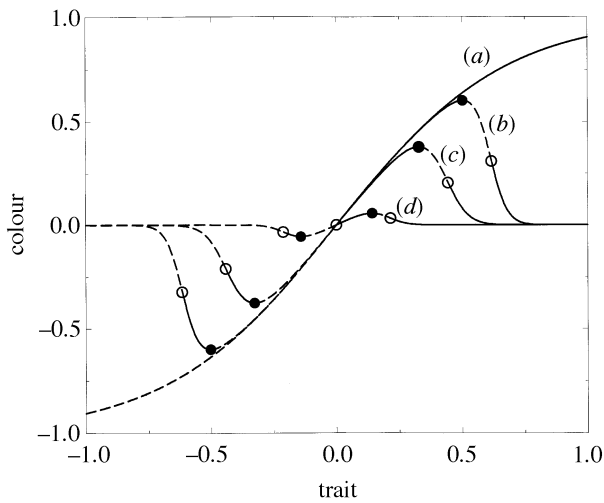


Figure 1. Trait-to-colour function $C(t)$ for different values of water turbidity a . Line (a), clear water, $a = 0$; line (b), $a = 0.01$; line (c), $a = 1.0$; line (d), very turbid, $a = 100$. Other parameters are set as $\sigma_p = 0.075$, $\sigma_k = 0.12$, $\mu = 0.03$ and $l = 0.5$ (see Appendix A); solid lines denote regions where $\Delta > 0$, for dashed lines $\Delta < 0$. Stable points are indicated by solid circles, whereas open circles denote unstable points.

For $t\Delta > 0$, females on average prefer a male trait that is more extreme than the average trait value in the population. Therefore the population is likely to evolve to more extreme trait values, whereas the opposite is true for $t\Delta < 0$. Near points $(t, C(t))$ where Δ changes sign, i.e. where C' or C'' changes sign, we can expect either speciation by runaway processes (unstable points, $C'(t)C'''(t) < 0$ and $C''(t) = 0$) or fusion of species (stable points). These conditions illustrate the importance of the shape of the trait-to-preference function.

For linear C , the quantity Δ equals zero everywhere along C . In this case, evolution along the trait-to-preference function is neutral in the absence of stabilizing natural selection on male trait.

For our particular cichlid case it is possible to derive an expression for C , using a simplified representation of underwater light conditions (see Appendix A). Figure 1 shows a graph of the trait-to-colour function. Note the unstable points around which the function is locally sigmoidal. For increasing turbidity, a , the shape of C changes smoothly: the unstable point at the origin becomes enclosed by stable points. This will have a profound influence on speciation and extinction processes.

(b) Speciation and extinction

Considering the results obtained in the previous section, the shape of the trait-to-colour function in clear water allows for sympatric speciation around the point $t = p = 0$. Figure 2 shows a typical speciation event. In turbid water the humps of the trait-to-colour function become more shallow and they approach the origin, which constrains the extent of the Fisher runaway process.

Starting from species evolved under clear-water conditions, an increase in turbidity leads to a decrease in the number of species, by fusion of species near stable points and extinction of species whose skin coloration can no longer be distinguished from the background. This

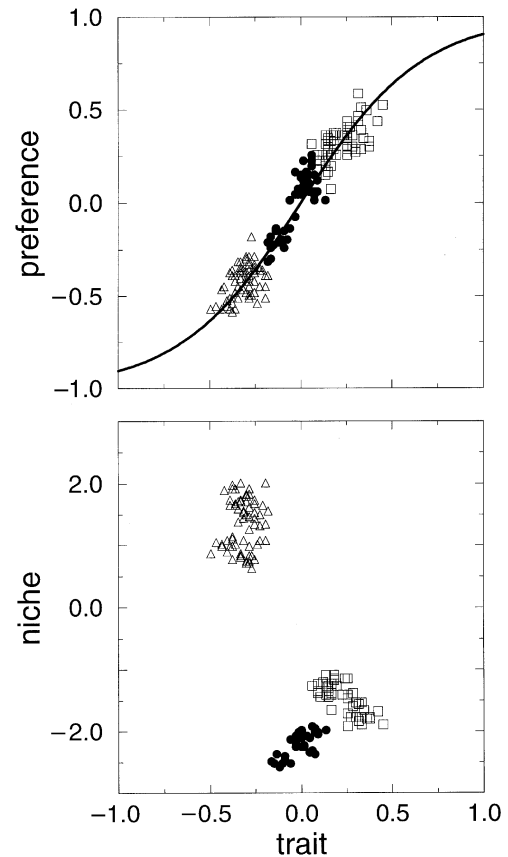


Figure 2. A typical speciation event. Different symbols denote different species. The species marked by filled circles is about to split into two daughter species. The species marked with triangles consists of two sub-clusters that have just fused. Note that all species occur on the trait-to-colour function (solid line in trait-preference space), as mentioned above.

occurs for t -values falling in the tails of $C(t)$ (figures 1 and 3). Note that the number of species decreases rapidly and permanently with increasing turbidity, whereas the total number of individuals N first collapses owing to extinction of extremely coloured males, but later on recovers to the original level again. In control simulations without sexual selection, N reaches the same order of magnitude, whereas the average number of species never exceeds two (data not shown).

Around unstable points, disruptive selection on mate choice occurs, which creates large intraspecific variance. Because of this, gene flow between the extremes of the character distribution of a single species is limited. Character displacement in niche space simultaneously rescues the two sub-populations from competitive exclusion—this reduces intraspecific gene flow even more—after which the Fisher process separates the two sub-populations, which evolve into different species.

Around stable points fusion of species occurs, which reduces the diversity. The disruptive or attractive force of these special points depends on the local curvature of the trait-to-colour function, which again depends on the turbidity of the water. In transparent water the trait-to-colour function declines steeply near stable points. This promotes the breaking up of species along the niche dimension by extinction of parts of the population owing to the difficulty of finding a suitable mate (for species near steep parts of the trait-to-colour function, the Allee

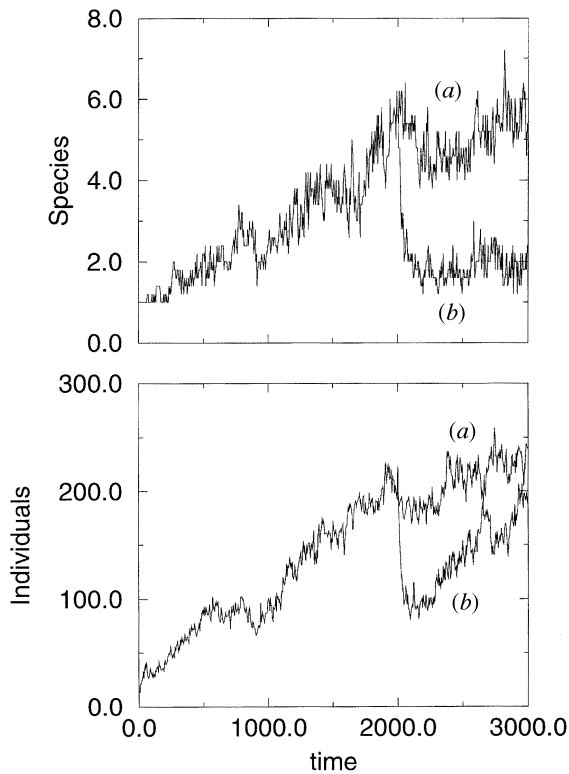


Figure 3. Number of species and individuals averaged over five runs. Line (a), without eutrophication, $a = 0.01$; line (b), with eutrophication, from time 2000 to 3000, a increases linearly from 0.01 to 100. Common parameters are $\pi_d = 0.002$, $c = 0.03$, $\eta = 0.01$, $\sigma_c = 0.06$, $\sigma_n = 0.06$, $\sigma_m = 0.06$, $\sigma_t = 0.04$, $\sigma_p = 0.04$, $\sigma_x = 0.04$ and $\sigma_s = 3.0$. For other parameters see figure 1.

effect is more severe). In turbid water the humps of the trait-to-colour function are shallow, which promotes the fusion of species along the niche dimension. In this case, intraspecific niche variation tends to be very large.

In this model, speciation is a very dynamical process. Reproductive barriers between species are low, so species continuously form and fuse, leading to reticulate evolution. The number of species that can coexist is limited by the amount of species that fit on the trait-to-colour function. Overlapping species often fuse if their niche differences are not large enough. Thus, intraspecific variation is an important factor determining maximal diversity. For smaller intraspecific variation the number of species that fit on the trait-to-colour function increases. The quantity Δ , however, will decrease with smaller variation (σ), which makes sexual selection less powerful, resulting in fewer speciation events.

4. DISCUSSION

The results presented here provide an explanation for both the high speciation rates in cichlids and the recent extinction of rock-dwelling cichlid species described by Seehausen *et al.* (1997). In our model, sexual selection and niche differentiation are required in the process of speciation. Sexual selection promotes the splitting of species, whereas niche differentiation prevents the extinction of species by competitive exclusion. Note that the scale σ_c required for niche differentiation is several times smaller than the intraspecific niche variance. Thus

speciation itself cannot be attributed to the niche differentiation in our model.

However, our results are not limited to this particular case. In all cases where the trait-to-preference mapping possesses unstable points, we expect results to be qualitatively similar. Note that well-known trait-to-preference mappings, such as ‘best of N’ (O’Donald 1980) and ‘open-ended female mating preferences’ (Lande 1981) are within this class of functions, provided that evolution in multiple directions is possible. The common feature of these functions is that females on average choose male traits that are more extreme than the average in the population.

As already mentioned, for linear trait-to-preference mappings in the absence of direct selection forces, evolution along the trait-to-preference function is neutral. This feature of a neutral line of equilibria has been observed in many Fisher runaway-process models (Lande 1981; Kirkpatrick 1982; Bulmer 1989), but, of course, it is a degenerate feature (Bulmer 1989; Maynard Smith 1991). Iwasa & Pomiankowski (1995) already showed some unexpected features of the evolution of the population means \bar{t} and \bar{p} under the Fisher process using a nonlinear trait-to-preference mapping. Our model tracks the full distribution of trait and preference and we show that in that case a nonlinear trait-to-preference mapping can produce prolific speciation and/or extinction. Our derivation of the trait-to-colour function from physical principles shows that the required nonlinearity is present in this particular case. In addition, this type of nonlinearity may not be an unreasonable assumption in general.

The model shows that sympatric speciation is possible under the weak assumptions we have made. The strict sympatry assumed in this model is of course a worst-case scenario. Spatial structure and local interactions will reduce gene flow between distant individuals, which will enhance the speciation process. Including niche space as well as true space will accelerate the evolution of diversity even more, as competitive exclusion between daughter species and fusion of species becomes less likely.

The same is true for sexual selection on several male characters at the same time, e.g. colour, size and brightness. This would effectively increase the dimensionality of the trait-to-preference mapping, which enlarges the number of directions a runaway process can take and increases the maximal possible distance between species.

APPENDIX A. TRAIT-TO-COLOUR MAPPING

Although possible, we refrain from a detailed, physically correct derivation and will use only the basic principles of reflection and scattering of light. In our model mate choice depends only on the hue of the reflected light, not on its brightness.

Starting from a flat light spectrum $I_0(\lambda) \equiv 1$ above the water surface, light of wavelength λ penetrating some distance d into the lake will have a spectrum given by $I_d: \lambda \rightarrow \exp[-a\varepsilon(\lambda)]$, where a is proportional to d and to the concentration of an absorbing and scattering substance A, which comprises algae and small scattering particles.

Near its wavelength of maximal absorption and scattering, arbitrarily put at $\lambda = 0$, the extinction coefficient of A, $\varepsilon(\lambda)$, is taken to be $\varepsilon : \lambda \rightarrow \lambda^2$. For simplicity we assume that at depth d , light has equal intensity in all horizontal directions (equal intensity assumption).

Light travelling horizontally from a reflecting surface (male cichlid) to the eye of a female cichlid will be partly transmitted ($T(\lambda)$). Furthermore, light from all directions can be scattered ($S(\lambda)$) into this optical path. The reflection coefficient $R(\lambda, t)$ is a function of male trait t and λ .

The light finally penetrating the female eye ($E(\lambda, t)$) equals

$$E(\lambda, t) = I_d(\lambda)(R(\lambda, t)T(\lambda) + S(\lambda)). \quad (\text{A1})$$

For a surface with $R(\lambda, t) \equiv 1$, it follows from the equal-intensity assumption that $E(\lambda, t) = I_d(\lambda)$ which implies $S(\lambda) = 1 - T(\lambda)$. $T(\lambda)$ is given by

$$T(\lambda) = \exp(-l a \varepsilon(\lambda)), \quad (\text{A2})$$

where l introduces a characteristic distance of mate recognition. $R(\lambda, t)$ is taken to be Gaussian:

$$R(\lambda, t) = \exp\left(-\frac{1}{2}\left(\frac{\lambda - t}{\sigma_p}\right)^2\right). \quad (\text{A3})$$

The minimal assumption for the visual system of cichlids is that they have a two-dimensional colour space, which requires a minimum of two cone types. The action spectra of the cones are again Gaussians:

$$K_1(\lambda) = \exp\left(-\frac{1}{2}\left(\frac{\lambda - \mu}{\sigma_k}\right)^2\right), \quad (\text{A4})$$

$$K_2(\lambda) = \exp\left(-\frac{1}{2}\left(\frac{\lambda + \mu}{\sigma_k}\right)^2\right). \quad (\text{A5})$$

Note that this induces a non-trivial symmetry in the problem, which simplifies further computations. Results, however, do not depend crucially on this symmetry. The output $O_i(t)$ ($i = 1, 2$) of cone i is obtained by integrating the product of $E(\lambda, t)$ and $K_i(\lambda)$ over all λ .

Within colour space, the chromaticity line is chosen to be $O_1 + O_2 = 1$, and colours are represented as

$$C(t) = \frac{O_1(t) - O_2(t)}{O_1(t) + O_2(t)}. \quad (\text{A6})$$

By substituting all expressions listed above and solving the integrals we obtain the trait-to-colour function

$$C(t) = \frac{\exp\left(-\frac{\alpha_1(t)}{2}\right) - \exp\left(-\frac{\alpha_2(t)}{2}\right)}{\exp\left(-\frac{\alpha_1(t)}{2}\right) + \exp\left(-\frac{\alpha_2(t)}{2}\right) + 2\sqrt{\beta_1}\exp\left(-\frac{\alpha_3}{2}\right) - 2\sqrt{\beta_2}\exp\left(-\frac{\alpha_4}{2}\right)}, \quad (\text{A7})$$

where

$$\alpha_1(t) = \frac{2a(l+1)(t^2\sigma_k^2 + \mu^2\sigma_p^2) + (t-\mu)^2}{2a(l+1)\sigma_k^2\sigma_p^2 + \sigma_k^2 + \sigma_p^2}, \quad (\text{A8})$$

$$\alpha_2(t) = \frac{2a(l+1)(t^2\sigma_k^2 + \mu^2\sigma_p^2) + (t+\mu)^2}{2a(l+1)\sigma_k^2\sigma_p^2 + \sigma_k^2 + \sigma_p^2}, \quad (\text{A9})$$

$$\alpha_3 = \frac{a\mu^2}{a\sigma_k^2 + 1}, \quad (\text{A10})$$

$$\alpha_4 = \frac{a(l+1)\mu^2}{a(l+1)\sigma_k^2 + 1}, \quad (\text{A11})$$

$$\beta_1 = \frac{2a(l+1)\sigma_k^2\sigma_p^2 + \sigma_k^2 + \sigma_p^2}{\sigma_p^2(2a\sigma_k^2 + 1)}, \quad (\text{A12})$$

$$\beta_2 = \frac{2a(l+1)\sigma_k^2\sigma_p^2 + \sigma_k^2 + \sigma_p^2}{\sigma_p^2(2a(l+1)\sigma_k^2 + 1)}. \quad (\text{A13})$$

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